Feeding of a Dorid Nudibranch, *Diaulula sandiegensis*, on the Sponge *Haliclona permollis*

BY

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(1 Text figure)

INTRODUCTION

A LARGE PERCENTAGE of the dorid nudibranchs are known to feed almost exclusively upon sponges (YOUNG, 1970), and an excellent background discussion of their diet specificity is presented by THOMPSON (1964). In some cases, such as *Rostanga pulchra* feeding on *Ophlitaspongia pennata*, the relationship is specific (COOK, 1962). In other cases the nudibranch is associated with closely related sponges, as for example the preference of *Rostanga rubicunda* for the sponges *Microciona coccinea, Ophlitaspongia seriata,* and *Holoplocamia neozelanicum* (AYLING, 1968). Similarly, closely related nudibranchs are associated with the same species of cosmopolitan sponge. For example, 3 species of nudibranch, *Archidoris montereyensis* on the Pacific coast (COOK, *op. cit.*), *A. tuberculata* in the North Sea (WOLTER, 1967), and *A. pseudoargus* on the shores of Great Britain (THOMPSON, *op. cit.*) are attracted to and specifically feed on the cosmopolitan sponge *Halichondria panicea.* The adequacy of this specific diet for growth has been demonstrated by CAREFOOT (1967), who measured rapid growth of *Archidoris* feeding on *Halichondria panicea.* COOK (*op. cit.*) and AYLING (*op. cit.*) have demonstrated that attraction of a nudibranch towards the sponge prey is chemical.

During a seasonal study of the environmental influences on growth and reproduction of a sponge population on the Central Oregon Coast (ELVIN, 1976), a relationship between the purple sponge, *Haliclona permollis*, and the dorid nudibranch, *Diaulula sandiegensis* (Cooper, 1863), became apparent. The keyhole limpet, *Diodora aspera* (Rathke, 1833), was also found to be a grazer on this sponge. COOK (1962) mentioned that the nudibranch and the purple sponge might be associated. However, BERTSCH *et al.* (1972) in a 5-year survey of nudibranchs on the shores of San Mateo County, California, did not report such a relationship although *Diaulula sandiegensis* was very common and *H. permollis* occurs in that region. MARCUS (1961) reported this nudibranch to range from San Diego to the Aleutian Islands and the stomachs of those from California to sometimes contain bits of keratose sponge.

It is the purpose of this paper to document the relationship of *Diaulula sandiegensis* and the purple sponge, *Haliclona permollis*, by presenting several quantitative aspects of the association and to establish the chemical attraction of the nudibranch to the sponge. The paper also reports on several growth and feeding observations.

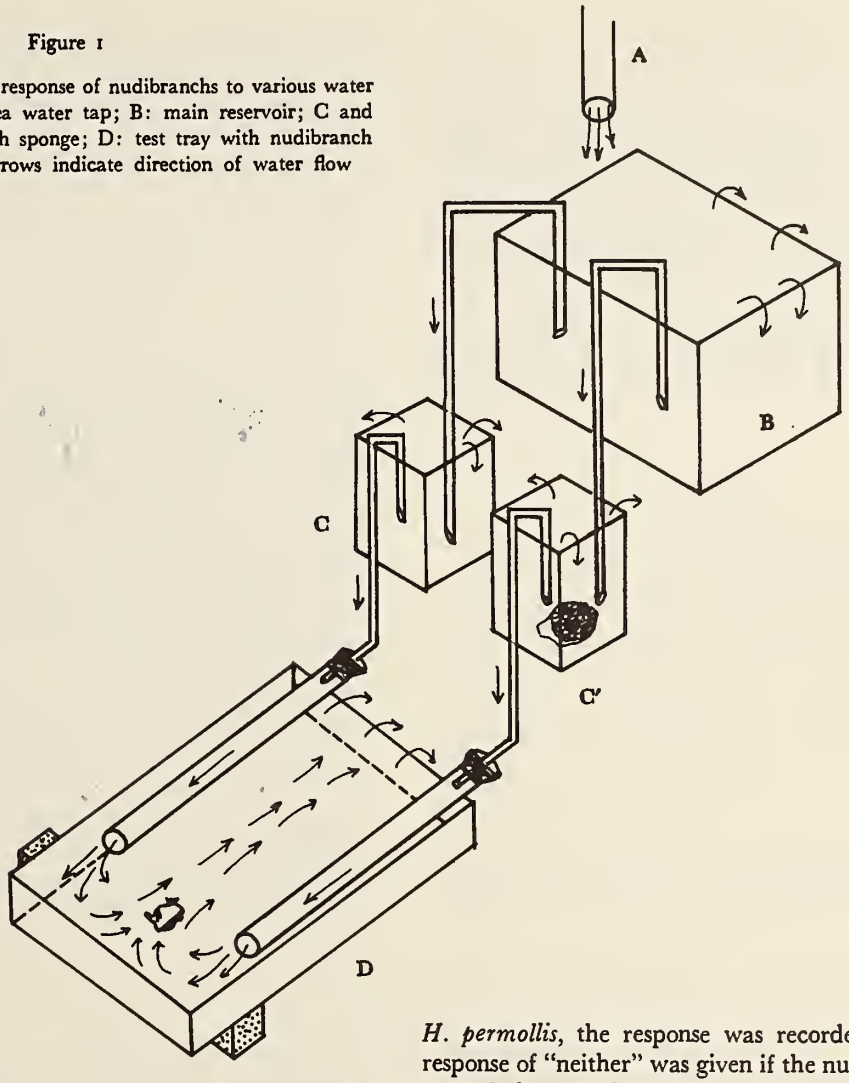
MATERIALS AND METHODS

The study area was located on Yaquina Head on the Central Oregon Coast, and both field and laboratory observations were carried out from March to July. The distance of every *Diaulula* encountered during low tide exposure from the nearest patch of *Haliclona permollis* was measured. Stomach contents of 3 specimens each of 2 grazers, *Diaulula sandiegensis* and *Diodora aspera*, collected at random from the field, were examined and the amounts and type of sponge spicules noted.

Chemotactic response towards sponges was tested using a glass variation of a Y-tube system (DAVENPORT, 1950) as shown in Figure 1. Both sides were supplied with sea water from the laboratory system taken from Yaquina Bay, and the reservoirs maintained a constant and equal current flow in each tube. The lower tubes were large enough to allow complete entry of the mollusks. Equal masses (3 - 5 cm^3) of uninjured sponges were placed in one or both of the sample chambers. A total of 12 nudibranchs 3 - 4 cm in length were placed in the test tray heading into the convergence of the 2 sample cur-

Figure 1

Apparatus for testing the response of nudibranchs to various water samples. A: laboratory sea water tap; B: main reservoir; C and C′: sample chambers with sponge; D: test tray with nudibranch in starting position. Arrows indicate direction of water flow



rents. A particular specimen was used for as many as 3 trials. Only nudibranchs starved for 1 or 2 days were found to be responsive. After each trial the tubes and glass tray were washed and the sponges switched to the other chamber. Three common sponges, *Halichondria panicea*, *Haliclona permollis*, and an unidentified white species of *Haliclona* from the intertidal region where the mollusks are found were used.

Four types of responses by the mollusk were possible. If the nudibranch crawled up the tube with water from the chamber containing *Haliclona permollis* within 20 minutes, the response was considered positive. Usually such a reaction occurred within a few minutes. If the mollusk crawled up the tube with water from a sponge other than *H. permollis*, the response was recorded as "other." A response of "neither" was given if the nudibranch crawled around the tray for an hour without moving up either tube, and "negative" if the mollusk crawled over the side and out of the tray.

From April 26 until July 9, observations of nudibranch feeding upon *Haliclona permollis* were carried out by leaving 8 specimens of *Diaulula,* ranging in size from 12 mg to 1450 mg in finger bowls containing an excess of sponge. At weekly intervals the nudibranchs were drained on damp towels and the damp-dry weight was measured to the nearest 1/10 mg. Sea water temperature during this period corresponded to that in the field and ranged from 9.1° to 15.1° C. Samples of sponge and of nudibranch feces were weighed after drying at 68° C and ashing at 580° C in a muffle furnace to obtain dry and ash weights, respectively (Paine, 1964).

RESULTS

Examination of stomach contents revealed that most of the recognizable particulate material in the *Diaulula* stomach was siliceous spicules from *Haliclona permollis* rather than from the white haliclonid which grows in the same area. The *Diodora* stomach contained quite a heterogeneous mixture of particulates including sponge spicules of several species.

Table 1 presents data supporting the association of *Diaulula* and *Haliclona permollis* in the field. In most cases the nudibranch was found within 2cm of the sponge. In contrast, *Diodora*, which is found in the same habitat, appears to be less restricted to areas of the purple sponge. Two specimens of *Diaulula* were found on the white haliclonid and these nudibranchs were of a much lighter color than the usual purple-tan background color of this species.

The results of the chemotactic study are shown in Table 2. There was no indication of a rheotactic response since the dorids never crawled up the tubes with only sea water currents. The mollusks were obviously able to distinguish between the water from the *Haliclona permollis* chamber and a control quite quickly, while their responses towards the water from other sponges were weakly positive. When given a choice between *Halichondria panicea* and *Haliclona permollis*, the nudibranchs were able to distinguish the water from the purple sponge 50% of the time, but some confusion in their decision was evident. The presence of the white haliclonid in one chamber apparently nullified any response towards the purple sponge. The 2 specimens of *Diaulula* found feeding on the white haliclonid in the field showed a positive response for this sponge, but none for *Haliclona permollis*.

The measurements on the growth of young nudibranchs resulted in an average specific growth rate of 2.4% per day and ranged from 1.3 to 4.2%. The food, *Haliclona permollis*, was found to consist of about 45% oxidizable organic material per dry weight. A damp-dry sponge has the following composition: 85% water, 6% organics, and 9% inorganic spicules. The feces of the nudibranch contained 16% dry weight of oxidizable organics. Calculation

Table 1

Association between two molluscan grazers and the sponge, *Haliclona permollis*, at low tide at Yaquina Head, Oregon.

Distance from nearest sponge	Grazer	
	Diaulula sandiegensis	*Diadora aspera*
0 to 2.0cm	28	4
2 to 5cm	—	4
5 to 15cm	1	2
15 to 30cm	4[1]	3
more than 30cm	2	—

[1]2 feeding on a white Haliclonid

Table 2

Behavior of *Diaulula sandiegensis* in the presence of sponges.

Choice presented	Number		Nudibranch Reaction			
	Individuals	Trials	*Haliclona permollis* (positive)	Other sponge	Neither sponge	Negative
0 vs 0	4	4	—	—	4	—
0 vs *Haliclona permollis*	7	12	12	—	—	—
0 vs *Halichondria panicea*	5	7	—	2	4	1
0 vs *Haliclona* sp. (white)	4	4	—	1	3	1
Haliclona sp. (white) vs *Haliclona permollis* (purple)	4	4	—	—	4	—
Halichondria panicea vs. *Haliclona permollis*	4	6	3	1	2	—
0 vs *Haliclona permollis*[2]	1	2	—	—	2	—
0 vs *Haliclona* sp.[2] (white)	1	2	—	2	—	—

[2]The nudibranchs used in these tests were found feeding on the white haliclonid in the field.

of the assimilation efficiency from the above data using the method of Conover (1966) gave a value of 77%. Microscopic examination of the feces showed that the remaining organic material was essentially the spongin which holds the spicule framework together. Under laboratory conditions, adult nudibranchs in the size range of 4cm were capable of consuming 1 cm^2 of 2½ mm high *Haliclona permollis* per day.

DISCUSSION

The observations in this study verify that *Diaulula sandiegensis* and *Haliclona permollis* are associated in a close grazer-prey relationship and that *H. permollis* is the principal food of the nudibranch at Yaquina Head, Oregon. Most of the nudibranchs were found on or near the purple sponge, and the few that were found at further distances may have been displaced by rough surf. However, the mollusks are not completely restricted to *H. permollis* since 2 specimens were found feeding on the white haliclonid. In well protected, shaded areas the white haliclonid is frequently found growing next to the purple sponge and these sponges are undoubtedly competing for substrate in this microhabitat, but in exposed areas *H. permollis* is found alone or growing next to and over *Halichondria panicea.*

Diaulula can distinguish between closely related species of sponges and certainly has a preference for *Haliclona permollis*, but it appears this preference may be influenced by other factors since those collected from the white haliclonid chose it over *H. permollis* during the chemotactic test. The function of such behavior in an environment filled with other chemical stimuli mixed by a rough surf is unclear. If the chemotactic response is used to locate food, then the immediate response noted in the laboratory is of value, but the presence of other sponges appears to interfere with efficient location of the purple sponge. It may also act to keep the nudibranchs in the area of the sponge upon which they are grazing and whose tissues they efficiently convert to their own. However, since the chemotactic response was weak or lacking in well-fed specimens, such a purpose becomes questionable.

The choices by *Diaulula* detected in this study would suggest specific dissolved or particulate attractants are released by the sponge. The construction of the apparatus is such that the probability of crawling up the tubes by chance is very small. There is some attraction for any sponge but it would not necessarily lead to feeding and therefore would be a mistake on the part of the mollusk. The amount of data is limited but it appears that species closely related, for example the 2 haliclonids, confuse the nudibranch and it cannot locate the sponge. However, this does not explain why neither of the sponge waters was chosen. When more distant species are presented, such as *Haliclona permollis* and *Halichondria panicea*, the mollusk can make the "proper" choice although its ability to do so is impaired. Presumably these differences reflect chemical differences of the sponge species. The available studies have not emphasized this aspect of the problem. Wolter (1967) demonstrated positive reactions towards nonspecific substances such as starch, glycogen, glycerol, and albumin. Navoni (1972) used various irritants to test chemosensory abilities of several nudibranchs. He also found sea water extracts from their prey hydroids to produce positive responses.

Haliclona permollis serves as an adequate diet for the growth of *Diaulula*. A specific growth rate of 2.4% per day for the young specimens is similar to the 1.7% found by Carefoot (1967) for *Archidoris* feeding on *Halichondria panicea*. The difference may be due to the percentage of organic material, 30% and 45% for *Halichondria panicea* and *Haliclona permollis*, respectively. Essentially all of the cellular material is removed from the sponge, and the spongin and spicules remain. The feeding rate of 1 cm^2 per day for the 3 to 4cm adults yields about 15 mg of organics or with 77% assimilation about 12 mg of organics per day. This value is low compared to data for *Archidoris* (Carefoot, *op. cit.*). It is possible that at certain times of the year the feeding rate is much higher. It should be recalled that this rate was determined in the laboratory where there is no interruption by tidal exposure and waves.

The nudibranch feeding rate is also of consequence to the prey population. If the adults are feeding at the above rate or greater in the field, the sponge population would require a standing stock of 100 cm^2 with a production rate of 1 $mm^2/1cm^2$/day as previously found by Elvin (1976) to maintain itself against grazing. Although the population as a whole appears to be sufficient in size to withstand this grazing pressure, individual patches are rarely this large and the nudibranchs which frequently congregate probably do clear areas and must move to others. Quantitative data on the annual changes in both nudibranch and sponge densities will be required.

SUMMARY

1. At Yaquina Head, Oregon, the dorid nudibranch, *Diaulula sandiegensis*, is associated with the purple sponge, *Haliclona permollis*.
2. *Diaulula* has a preference for *Haliclona permollis* and can locate it by chemotaxis.

3. The chemotactic response is influenced by the presence of other sponges and the previous nutritive condition of the mollusk.
4. *Haliclona permollis* is an adequate food source for *Diaulula* and allows young individuals to grow at a rate of 24 mg/g damp weight/day.

ACKNOWLEDGMENTS

This work is the result of research sponsored in part by the Oregon State University Sea Grant College Program, supported by NOAA Office of Sea Grant, Department of Commerce, under Grant # 04-3-158-4. The United States Government is authorized to produce and distribute reprints for governmental purposes notwithstanding any copyright notation that may appear hereon.

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